Unusual organization of scent glands in *Trogulus tricarinatus* (Opiliones, Trogulidae): evidence for a non-defensive role

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Abstract. The morphology of the scent glands of *Trogulus tricarinatus* (Linnaeus 1767) (Trogulidae), a small, soil-dwelling opilionid species, was investigated by means of serial histological semi thin-sections. The glands constitute paired prosomal glandular sacs that open to the body surface via one pore (ozopore) on either side of the body, dorsally adjacent to coxae I. Consistent with the generally recognized organization of scent glands in Opiliones, an anterior non-secretory region of the reservoir could be distinguished from a posterior secretory area, the latter characterized by a thick vacuolated epithelium. However, there are several unusual scent gland features in *T. tricarinatus*. First, the ozopores are hidden, with each being surrounded by a kind of external secretion atrium formed by a dorso-lateral integumental fold (dorsal limitation), coxa I (ventral limitation), and a wall of projecting cuticular papillae (outer lateral limitation). A horizontal slit ("secondary opening") between the top of this wall and the dorsal integumental fold is externally visible. Secondly, no fluid, but solid spherical structures that may represent condensed secretion are found in the reservoirs. Thus, the secretion must pass through the external atrium before reaching the outside, perhaps as a gas produced by slow sublimation of solid secretion boli. Scent gland organization in *T. tricarinatus*, especially the findings of an external atrium around the ozopores, is not consistent with use in chemical defence, as is generally assumed for scent glands of Opiliones, but indicates a possibly non-defensive role.

Keywords: Exocrine glands, chemical defense, opilionids, Palpatores, Dyspnoi

Large prosomal exocrine scent glands, also called defensive or repugnatorial glands, are an important synapomorphic character of Opiliones (Martens 1978). Although large and conspicuous, scent glands have been examined in only a few detailed histological studies. Clawson (1988) described the scent glands of two sclerosomatid species, and the scent glands of a few ischyropsalidid species were investigated by Lopez et al. (1980) and Juberthie et al. (1991). Recently, an ultrastructural study on exocrine glands of *Cyphophthalmus duricorius* (Cyphophthalmi) was published (Gutjahr et al. 2006).

In general, opilionid scent glands are considered a means for defense (e.g., Martens 1978). This view is based on 1) the characteristic morphological organization of glands that clearly show an "allomonal-type" gland construction, comprising undivided, intima-lined, large-scale reservoirs along with a central orifice and 2) emission of secretions that, in most cases, is inducible by mechanical disturbance and frequently is followed by distinct behavioral steps such as "leg dabbing" (sensu Juberthie 1961). In many Laniatores, cuticular grooves lead backwards from scent gland orifices and serve to divert the secretion on the body surface, leading to the generation of a protective chemical shield around the body (summary in Gnaspini & Hara 2007). Finally, and possibly most importantly, 3) the repellent properties of secretions against potential opilionid predators have been proven in bioassays and by behavioral observations, at least for some model species (e.g., Eisner et al. 2004; Willemart & Pellegatti-Franco 2006).

While these scent-gland properties seem to be consistent in Cyphophthalmi and Laniatores, the scent gland features of a

large part of Palpatores, namely in some phalangiids and in the Dyspnoi, are quite cryptic. Glands and glandular openings (ozopores) may be inconspicuous and some species are apparently reluctant to discharge secretion, even in cases of heavy mechanical treatment (e.g., Kaestner 1931–1941). Especially in representatives of Dyspnoi, such as in Trogulidae, a discharge of secretion has never been observed (Pabst 1953).

Recent studies have shown that the functional repertoire of opilionid scent glands may exceed pure chemical defense. Such additional functions may include the production of antibiotics (e.g., Estable et al. 1955; Fieser & Ardao 1956), alarm pheromones (Machado et al. 2002), aggregation and sex pheromones or pheromones for territorial marking (Bishop 1950; Holmberg 1986; Juberthie et al. 1991). Exocrine glands of arthropods producing the latter types of pheromones, however, typically exhibit a glandular organization distinctly different from opilionid "allomonal"-type scent glands (e.g., Percy-Cunningham & MacDonald 1987). Thus, espeeially with respect to the scent glands of certain Dyspnoi (such as non-scenting Trogulidae), a possible change of glandular function and role may not only be indicated by a reluctance to discharge secretion, but also by a distinctly different morphological organization of glands.

In the present study, we investigated the scent glands in a model, non-secretion discharging species, *Trogulus tricarinatus* (Linnaeus 1767) (Opiliones, Trogulidae), and we here report on its aberrant scent gland construction.

METHODS

Specimens of *Trogulus tricarinatus*, including adults of both sexes and juveniles, were collected from soil samples from different locations in Carinthia and Styria, Austria, by hand or

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using a Berlese apparatus. Specimens were fixed in Bouin's solution for 24 hours, washed, dehydrated, and embedded in LR-white soft grade (London Resin Company Ltd., Berkshire, England via Gröpl, Tulln, Austria). Blocks were sectioned using glass knives and a rotary microtome (Leica Jung 2065 Supercut, Leica, Vienna, Austria), leading to serial cross and longitudinal sections of 2.5 μm thickness. Sections were stained with toluidin blue (Lactan, Graz, Austria). Scent glands and surrounding structures were reconstructed from sections according to Honomichl et al. (1982) and by 3D-reconstruction software (Amira 4.1). For scanning electron microscopy (SEM), fixed, washed, dehydrated and air-dried specimens were mounted on aluminium stubs, sputtercoated (AGAR sputtercoater, Gröpl, Tulln, Austria), and examined with a Philips XL30 ESEM (Philips/FEI, Vienna, Austria) at high vacuum mode and 20 kV accelerating voltage.

RESULTS

Topography and size of glands.—One prosomal sac-like scent gland is situated directly beneath the integument on each side of the carapace. Each extends backwards 500–700 μm from the level of the first legs, which corresponds to 10 to 15% of the body length (Fig. 1). The glandular sacs (g) are rather narrow in their most anterior region (diameter about 50 μm), but reach a maximum width of more than 200 μm in more posterior parts. Only minor sex-related differences were noted and are limited to differences in shape due to spatial demands of the closely adjacent genital systems. In general, the sacs are moderately sinuate and laterally flattened (Figs. 1, 6, 7).

Glandular openings (ozopores) and "secretion atrium".—Ozopores (o) are oval-shaped with a maximum diameter of about 50 μm and are located nearly dorsal to the coxae of leg I (cx I). In adults, these openings are not visible externally but are hidden in a kind of secretion atrium (a). Specifically, this atrium (see Fig. 2) is built of 1) the dorso-lateral integumental folds (f) of the anterior carapace (= dorsal limitation), 2) coxa I (= ventral limitation), and 3) a heavy wall of cuticular papillae (= c and cp: outer lateral limitation). These papillae cover large parts of the cuticle and represent elongated, hollow, column-like structures, each 50–70 μm in height and about 30 μm in diameter ("Druesenwaerzchen" sensu Schwangart 1907). The cuticular papillae comprise the outer lateral wall of the atrium, each papilla bordering the next without a gap and projecting upwards from coxae I (Figs. 2, 9, 10). Only a narrow, sickle-shaped slit (so) of 5–40 μm width and 65–200 μm length between the dorsal integumental fold and the top of the wall of cuticular papillae remains open and can also be seen from the outside (Figs. 2, 8–11). This slit represents the external opening of the atrium, and thus, a kind of "secondary" opening of the scent glands. In addition, in the most anterior part of the atrium, its cavity is ventro-medially not completely closed but is connected to the camerostome through a groove. In general, the cavity of the atrium is spherical to egg-shaped, with a horizontal extension of about 140–190 μm; width and height of the cavity are about 40 and 200 μm, respectively. The inner surface of the atrium is covered with cuticular spines that mainly project from the ventral (coxa) and dorsal (integumental fold) walls. Scanning electron micrographs of the atrium and the secondary slit-like orifice, histological sections and a 3-D reconstruction of the atrium and
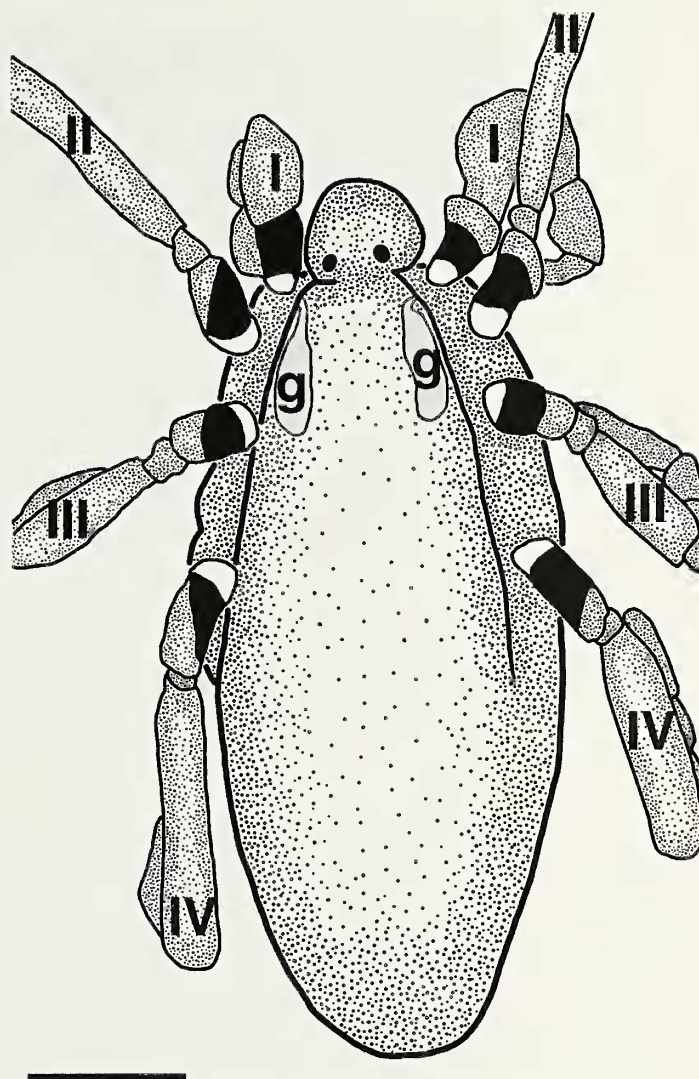

Figure 1.—Position, size, and shape of prosomal scent gland in *Trogulus tricarinatus* (semi-schematic). Male, dorsal view. Position of sac-like scent glands (g) is indicated. Abbreviations: I–IV = legs I–IV, g = scent gland. Scale bars = 1 mm.

adjacent structures are given in Figs. 2, 8–11. In juveniles, cuticular papillae (and thus, also the atrium itself) are lacking.

Reservoir: excretory duct, non-secretory and secretory areas.—Each scent gland mainly comprises a large intima-lined sac (g, reservoir) surrounded by non-secretory epithelium anteriorly and secretory epithelium posteriorly. The most anterior part also includes a short, narrow excretory duct (d) that latero-ventrally branches off the reservoir to reach the ozopores (Figs. 2, 6, 7). Muscles (m) attach at the inner side of the dorsal integument and extend transversely to the region of the duct (Fig. 2). They are only present in the most anterior region of glands, (i.e., in the narrow zone near the excretory duct and the pore orifice). A kind of "lid" (l, not further specified, multi-cellular tissue) seals the gland opening; the muscles, however, do not attach on the lid, but ventrally adjacent to it on the cuticle.

The non-secretory area of the glands (Fig. 3) either shows an intima layer only (= no epithelium visible) or, a bit more posterior, a single-layered epithelium (e). In the middle part of
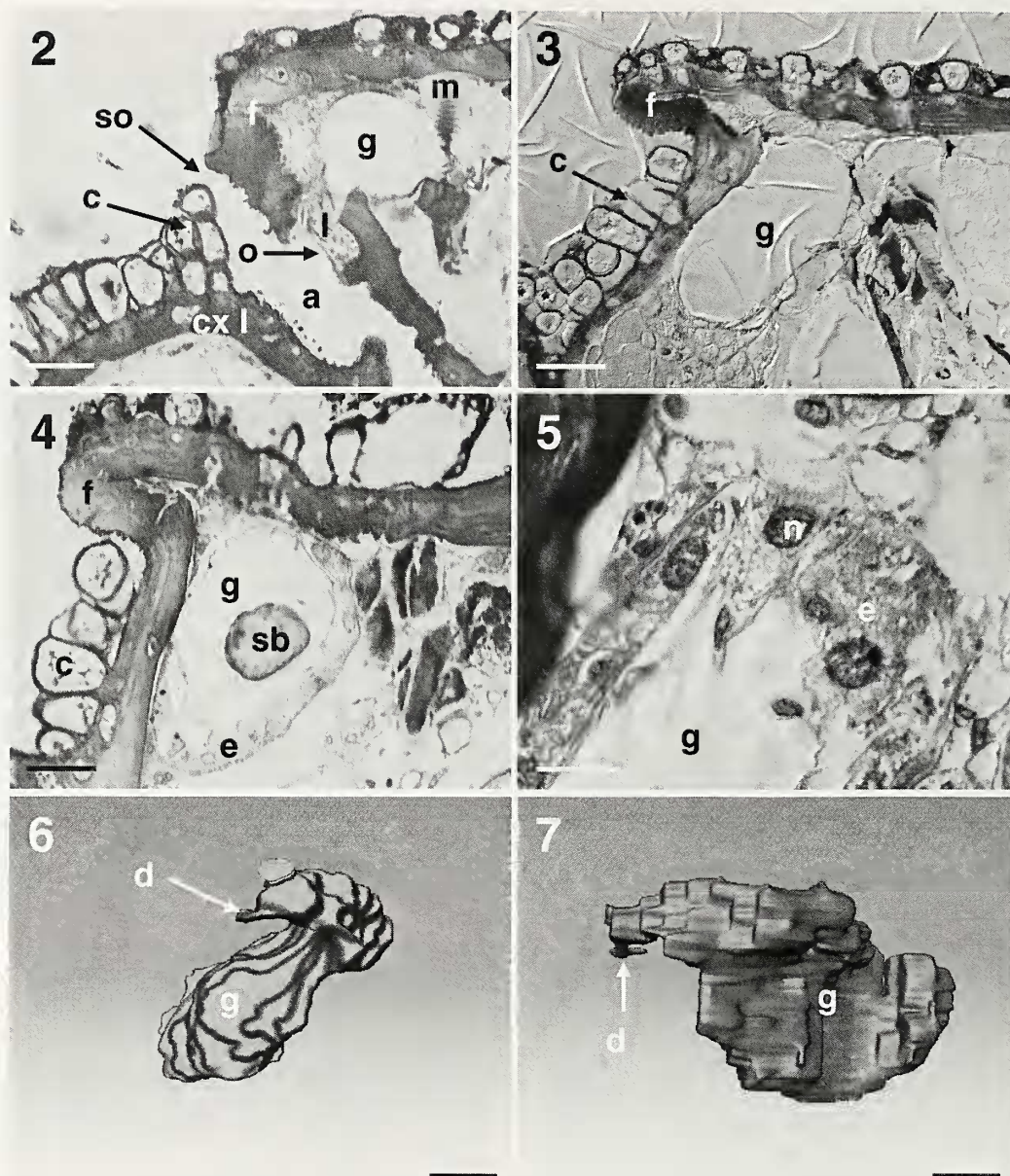
Figures 2–7.—Histological sections and reconstruction of scent glands in *Trogulus tricarinatus*. 2. Cross section through left scent gland (g) in its most anterior part at the height of coxae I (cx I); pore orifice (= ozopore, sealed by a lid) leads into the secretion atrium (a). In this region, the atrium is ventrally not completely closed (connecting to the camerostome); laterally it is bounded by a wall of cuticular papillae (c). Note the slit-like secondary opening (so). 3. Cross section through the anterior region of left scent gland, showing the non-secretory area. 4. Cross section, left scent gland in a more posterior region, showing the secretory area. Thick glandular epithelium (e) and secretion bolus (sb) visible. 5. Detail of secretory epithelium with grained and vacuolated epithelial cells (e) and large nuclei (n). 6, 7. 3D-Reconstruction of right scent gland from histological sections, surrounding structures omitted: 6. Frontal view; 7. Lateral view from the inner side. Abbreviations: a = secretion atrium, c = wall of cuticular papillae, cx I = coxa I, d = excretory duct, e = epithelium of scent gland reservoir, f = integumental dorsal fold of the carapace, g = scent gland reservoir, l = lid, m = muscles, n = nucleus of epithelial cell, o = scent gland orifice, sb = secretion bolus, so = secondary opening. Scale bars: 100 μm (6, 7), 50 μm (2–4), 10 μm (5).

the glands, the epithelial cells are small and flat, reaching a height of up to 10 μm and a width of 20–30 μm. These epithelial cells do not show apparent granulation or vacuoles when observed under the light microscope. The thickness and development of the epithelium as well as the folds of the intima distinctly increase from the middle part of glands to their posterior end. The posterior part obviously represents the secretory area of the glands (Fig. 4), as indicated by conspicuously large epithelial cells that are cuboidal (maxi-

mum height and width 60 μm) and show distinct plasmatic structures (large granules and vesicles) and large nuclei (*n* in Fig. 5). In this region, the intima protrudes in multiple folds into the reservoir lumen.

While the reservoirs appear to be largely empty (but not collapsed) in histological sections (at least, these do not contain stainable liquid secretion), a few (1–4) compact, slightly stainable spheres (sb) of about 50–70 μm in diameter could be found in the posterior part of the reservoirs (Fig. 4).
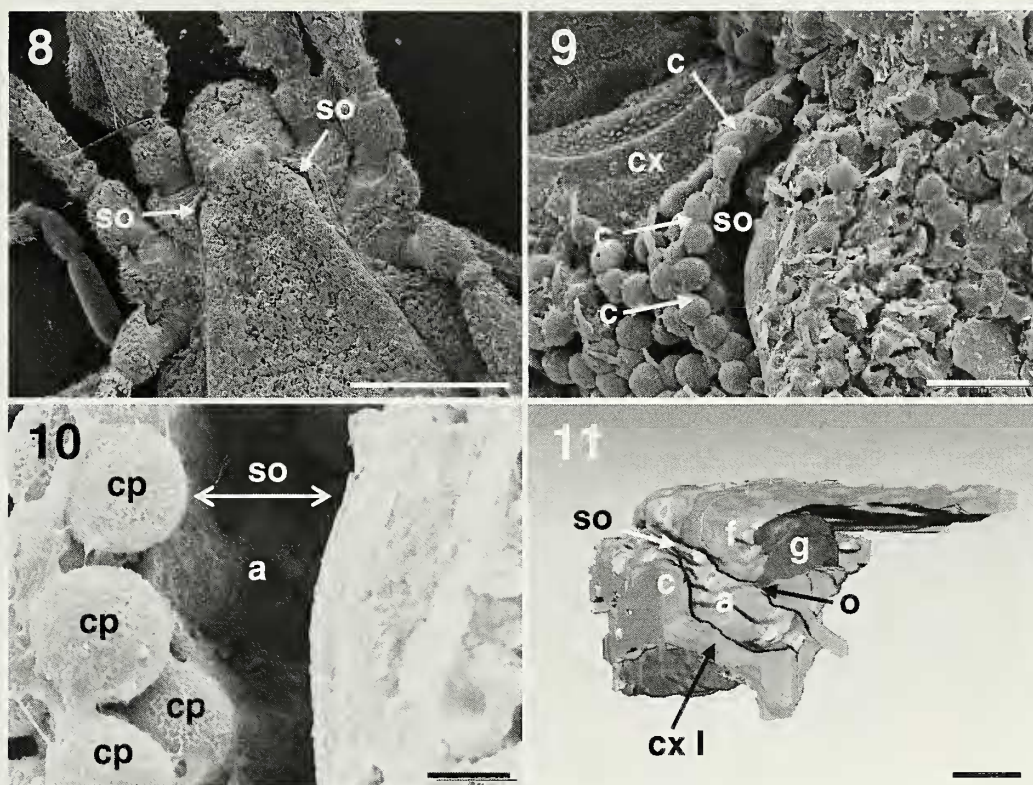
Figures 8–11.—Secretion atrium and secondary orifice in *Trogulus tricarinatus*. 8. SEM of the prosoma of a male individual, dorsal view. Arrows mark the secondary, slit-like orifice of the secretion atrium. 9. SEM, detail of left secondary orifice of secretion atrium. Note the outer, lateral wall of adjacent cuticular papillae that project from coxa I. 10. SEM, one fresh look into the secondary orifice. 11. 3D-Reconstruction of the right scent gland and surrounding integumental structures, including the secretion atrium (a) with secondary opening (so), antero-lateral view (reconstruction from serial cross sections). Opening of gland (ozopore, o) into the external secretion atrium (a) is visible. Abbreviations: a = secretion atrium, c = wall of cuticular papillae, cp = singular cuticular papilla, cx I = coxa I. f = integumental dorsal fold of the carapace, g = scent gland reservoir, o = scent gland orifice, so = secondary opening, Scale bars: 1000 μm (8), 100 μm (9, 11), 20 μm (10).

DISCUSSION

Internal organization of scent glands in *Trogulus tricarinatus*.—The internal organization of scent glands in *T. tricarinatus*, mainly comprising glandular sacs with central orifices, corresponds to anatomical data known from other Opiliones (e.g., Juberthie 1961, 1976; Clawson 1988; Gutjahr et al. 2006). Such general scent gland features obviously include large glandular reservoirs that are divided into a non-secretory and a secretory area and characterized by differentially developed glandular epithelium. The anterior area of the reservoirs in *T. tricarinatus*, showing intima or flat epithelial cells only, apparently corresponds to the non-secretory area of opilionid scent glands as, for instance, described in *Cyphophthalmus duricorius* Joseph 1868 (Cyphophthalmi) and in *Leiobunum* spp. (Phalangioidea: Sclerosomatidae) (Clawson 1988; Gutjahr et al. 2006). The flat cells may be classified as cuticle-supporting cells that are responsible for sustaining the thin intima that covers the lumen of the reservoirs. Furthermore, the available literature indicates that the secretory area of the scent glands (generally located in the posterior part of glands) consists of both small cuticle-supporting cells and large-grained secretory cells, with the latter cell type also being characteristic of the posterior area of glands in *T. tricarinatus*. Secretory cells in glands of *C. duricorius*, for instance, are reported to contain many mitochondria, lipid droplets, and granules, either being electron-lucent or electron-dense (Gut-

jahr et al. 2006); for *T. tricarinatus*, comparably structured secretory cells are expected but this remains to be studied by ultrastructural methods.

Gland construction vs. biological role in *Trogulus tricarinatus*?—As outlined above, opilionid scent glands are generally considered to show a morphological organization that is typical of defensive glands found in arthropods. By contrast, the scent glands of *T. tricarinatus* (and possibly other Trogulidae) exhibit a few peculiarities: ozopores are covered by a secretion atrium, a cavity between the cuticle and the cuticular papillae that cover the cuticle. Thus, in case of secretion discharge (if occurring at all), the secretion would have to pass through the atrium before reaching the body surface. Due to these morphological peculiarities, the secretion can be neither easily nor rapidly expelled nor transferred to a potential predator. To our knowledge, such an atrium surrounding or covering the scent gland orifices has not been described elsewhere in Opiliones. In scanning electron micrographs, the slit-like external openings of the atrium are clearly visible; these obviously represent secondary openings for potentially discharged secretion. Such atria along with (secondary) openings can also be found in other adult Trogulidae (unpublished observations), whereas these are clearly absent in juveniles. In these terms, a scanning electron micrograph of the ozopore of *T. nepaeformis* in Eisenbeis & Wichard (1985) is most likely derived from a juvenile individual.

In distinct contrast with *T. tricarinatus*, ozopores tend to be visible and easily accessible from the outside in most other Opiliones, and are especially conspicuous in Cyphophthalmi (i.e., openings are located atop protruding tubercles, perfectly suited for defense). Also the modes of secretion delivery appear to be especially well adapted for defense in Cyphophthalmi and Laniatores, where secretions are either extruded more or less forcefully from ozopores as fine jets or as droplets or are transferred to the offender by leg dabbing (e.g., Juberthie 1961, 1976; Eisner et al. 1971, 1977; Acosta et al. 1993; Gnaspini & Cavalheiro 1998;). In contrast, *T. tricarinatus* does not emit secretions when mechanically treated or squeezed (Pabst 1953; original observations). These peculiarities strongly suggest a non-defensive role for the glands.

Secretion and secretion chemistry in *Trogulus tricarinatus*?—
A further important argument against a defensive role of scent glands in *T. tricarinatus* concerns the presence and the (possibly solid) state of secretions. In general, defensive exocrine glands of arthropods produce and store liquid secretions, or at least, also contain solvents (diverse short-chain compounds) in which solid (or long-chain) compounds are dissolved. This situation is also realized in scent glands of the majority of Opiliones, even though rather viscous (but not solid) scent gland secretions have been reported from Laniatores. In Gonyleptidae, scent gland secretions are mixed up and diluted by enteric fluid before application (e.g., Eisner et al. 2004). Chemically, phenols and benzoquinones predominate within laniatorid secretions, while acyclic components and, at least in *Phalangium opilio* Linnaeus 1758, also naphthoquinones (Wiemer et al. 1978) are produced by phalangioids (for a summary see Gnaspini & Hara 2007). In Cyphophthalmi, both acyclic ketones and naphthoquinones are emitted (Raspotnig et al. 2005). No studies, however, on scent gland chemistry are available for Dyspnoi. This apparent lack of published information on Dyspnoi may be due, at least partly, to the production of a solid secretion, which leads to a "reluctance" or inability of the animals to discharge the secretion and to methodological difficulties in accessing them. So far, apart from *T. tricarinatus*, solid secretion boli in scent glands have also been found in some species of *Ischyropsalis* (Juberthie et al. 1991) but are expected to occur in further representatives of Dyspnoi, as well. For these solid secretion-producing Dyspnoi, a completely different, highly unusual system for emission of scent gland secretion may have evolved. Juberthie et al. (1991) speculated that solid secretion in scent glands may be released by slow sublimation and, thus, may be emitted as a gas. This mode of emission is currently classified as a distinct type, namely "the type which produces a scent without fluid production." Gnaspini & Hara (2007) considered this unusual mechanism of emission to be important for generating a chemical shield around the body, possibly protecting the emitter from predator attacks but also from microbes and fungi that are present in the subterranean environment.

In these terms, the slightly stainable spherical structures in the glandular reservoirs of *T. tricarinatus* may in fact represent a condensed (or crystalline) solid secretion, even though an artificial formation of these solid boli in the course of the histological preparation procedures (e.g., by precipitation or dehydration of secretion products) has to be considered as well. However, for the time being, the mechanisms of emission of presumably solid secretion (as described above) remain very speculative, the more than preliminary chemical investigation into scent glands of *T. tricarinatus* (based on hexane whole body-extracts) did not show any compounds accessible to gas chromatography (unpublished observation).

CONCLUSIONS

Taken together, the unusual gland construction (i.e., a secretion atrium covering the ozopores along with possibly solid secretion) and the observation that mechanical disturbance does not induce noticeable emission of secretion, strongly indicate a function other than chemical defence for scent glands of *T. tricarinatus*. More likely biological roles of scent glands in *T. tricarinatus* (and possibly also in other Trogulidae) may include territorial marking, as already proposed for subterranean ischyropsalidids (Juberthie et al. 1991), or even the production of aggregation pheromones (e.g., Bishop 1950; Holmberg 1986). Sexual communication, also often discussed (Pabst 1953), is probably not consistent with scent glands of *T. tricarinatus* as these glands do not show sexual dimorphism. In terms of an evolutionary interpretation of our findings, costly chemical defense may have become less important in the already well-defended trogulids (heavy sclerotization, soil incrustation, and cryptic lifestyle), and novel scent gland functions other than defense may have evolved.

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